Species Structure of the Gobiid Fish *Gillichthys mirabilis* from Coastal Sloughs of the Eastern Pacific[1]

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A RECENT ISSUE of *Systematic Zoology* (1960, vol. 9, nos. 3, 4) was devoted entirely to a symposium entitled "The Biogeography of Baja California and Adjacent Seas." One recurring theme was the affinity between forms occurring on the Pacific Coast in the Californian province (Hubbs, 1960: 134), and those in the northern part of the Gulf of California. Between these areas, in the main part of the Gulf, the fauna was said to differ, being primarily Panamic in origin (Garth, 1960; Hubbs, 1960; Walker, 1960).

The outer-coast species found in the upper Gulf of California are Pleistocene relicts, now trapped in a cul-de-sac of warm, tropical water (Hubbs, 1948: 463; 1960: 137). According to Walker (1960: 130), most of the northern species found there differ from their cognates on the Pacific Coast. As the symposium revealed, however, there has been no extensive study comparing populations of one species on the Pacific Coast with those of the same species in the Gulf of California.

The immediate objective of this investigation, although it was initiated before the symposium was conceived, was to establish the nature of the variation between populations of *Gillichthys mirabilis* Cooper. The goal was to ascertain the degree of differentiation of the form from the upper Gulf in relation to the over-all structure of the species. A brief study (Barlow, 1961*a*) of *G. seta* (Ginsburg) has served as comparative material to gauge the differences observed in *G. mirabilis*. *G. seta* is a close but distinct species restricted to an extreme rocky habitat found only in the upper Gulf.

G. mirabilis has been cited as one example of a species from the Pacific Coast which is also found in the upper reaches of the Gulf of California (Fig. 1). It occurs in the central region of the Gulf as well. There is a break in its distribution around Cabo San Lucas, however, separating the species into a Gulf group and a Pacific Coast group (details in Barlow, 1961*a*).

At the inception of the present investigation *G. mirabilis* from the northern part of the Gulf of California was considered by some ichthyologists to be a distinct species, *G. detrusus* Gilbert and Scofield. Differences of opinion existed (Barlow, 1961*a*), and the issue was clouded by comparisons with a third species, the then undescribed *Gillichthys seta*. As will be seen, the evidence supports the conclusion of Starks and Morris (1907: 227) that *detrusus* should be regarded as a synonym of *mirabilis*.

In 1930 *G. mirabilis* from the San Diego area in southern California was introduced into the Salton Sea. The fish has become well established in that odd saline lake in the Colorado Desert of California. This has proved to be a fortunate experiment.

ACKNOWLEDGMENTS

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ECOLOGY AND NATURAL HISTORY

The typical habitat of *mirabilis* is the intertidal coastal slough with its extensive mud flats. Less often it is a swampy lagoon, or slough, at the mouth of a dry river which most of the time is closed off from the ocean by a sand bar.

Salinity

The water in these habitats is of moderate to high salinity, hypersaline conditions being common. The maximum salinity where *mirabilis* has been recorded was 82.5 ‰ at "El Marino," north of San Felipe in the upper Gulf of California (Lars Carpelan, personal communication). The fish usually are absent where the water is fresh or only slightly brackish. Those kept in fresh-water aquaria were listless and died within 1–2 weeks, but this may have been due to the quality of the tap water. The activation time of the spermatozoa is quickest in water having a salinity of 35 ‰ (Weisel, 1948: 47).

Temperature

Aside from illumination, temperature is the one parameter of the environment to which it is related that changes more or less regularly with the latitude of the habitat. Local conditions, of course, may distort this temperature gradient. Furthermore, the Gulf of California has a climate different from that of the Pacific Coast. For these reasons, and in order to point out the extreme situation found at the Salton Sea, the meager temperature data available have been assembled and are presented in Table 1.

Air temperatures have been used instead of sea surface temperatures. In the backwaters and ponds where *mirabilis* occurs, the surface water temperatures tend to be correlated with air temperatures (Carpelan, 1957: 376; Barlow, 1958:

582), even when moderate tidal exchange takes place (personal observations).

Throughout the year on the Pacific Coast, air temperatures increase from north to south. The increase is more pronounced in summer than in winter. For example, San Diego is warmer than San Francisco by about 4–5 C during the summer, but is only 2–3 C warmer in the winter.

The protected Alviso ponds of southern San Francisco Bay, with their increased insolation, exhibit a special climatological situation (Carpelan, 1957: 376) that removes them from the normal gradient of temperature change associated with latitude. Air temperatures at the ponds during 1 year averaged almost 7 degrees higher than the long-range monthly means for San Francisco shown in Table 1. The climate at Alviso ponds evidently is warmer than at many truly coastal sloughs much further south.

In the Gulf of California region air temperatures increase from north to south during much of the year. But during the late, hot, summer season the situation is reversed and the mean air temperatures decrease, though only slightly, from north to south. However, the mean sea surface temperatures for August (Roden and Groves, 1959: 14) show no latitudinal trend whatsoever. Chiefly because of the reversal in the gradient of the air temperatures, the annual range of means is low in the south but is progressively greater to the north in the Gulf.

In the tidal sloughs of the Gulf of California where *mirabilis* normally is found, the summer increase from south to north in the range of water temperatures probably is augmented by the nature of the tidal change. The tidal range increases dramatically from south to north up the Gulf, reaching a maximum of 10 m at the head of the Gulf (Roden and Groves, 1959: 28). The sills of the sloughs usually are high. Thus as one proceeds north in the Gulf, the sloughs daily have a progressively longer pond phase. This means that the buffering effect of the tidal exchange will be less, and as a result the water temperatures in the sloughs will register still greater fluctuations.

The winter mean air temperatures at San Diego on the Pacific Coast, the central and northern Gulf of California areas, and the Salton

TABLE 1

MONTHLY MEAN AIR TEMPERATURES

| MONTH | PACIFIC COAST[1] | | SALTON SEA[2] | GULF OF CALIFORNIA[3] | | | | |
| | | | | West Coast | | East Coast | | |
	San Francisco 37° 48′N	San Diego 32° 34′N	33° 18′N	Mulege 26° 53′N	La Paz 24° 10′N	Guaymas 27° 55′N	Topolo-bampo 25° 36′N	Mazatlan 23° 11′N
January	9.3	12.5	12.0	14.0	18.2	17.7	18.6	19.3
February	11.6	13.5	13.0	16.0	19.2	18.9	19.7	19.4
March	12.9	14.4	17.5	17.8	21.3	20.7	20.1	19.7
April	13.4	15.2	20.5	20.1	23.2	22.8	22.2	21.3
May	14.1	16.9	24.5	22.9	25.5	25.5	25.0	23.8
June	14.9	17.8	28.0	27.2	27.2	29.1	29.1	26.4
July	14.8	19.9	30.5	30.5	30.0	29.8	29.8	27.5
August	15.1	20.3	31.5	30.4	30.3	30.5	29.7	27.6
September	16.7	19.4	29.5	29.0	29.0	30.2	29.7	27.5
October	15.7	17.8	24.5	24.6	27.0	27.3	27.8	26.7
November	14.0	15.9	18.5	19.5	23.2	22.6	24.0	23.5
December	10.4	13.6	13.0	14.9	20.0	18.6	19.7	20.6
Range	7.4	7.8	19.0	16.5	12.1	12.8	11.2	8.3

[1] Hubbs, 1948.
[2] Carpelan, 1958.
[3] Roden, 1958.

Sea are surprisingly similar. The summer temperatures, in marked contrast, diverge greatly. San Diego and San Francisco remain moderate, but the mean air temperatures exceed 30 C in the Gulf and Salton Sea areas.

The climate of the Salton Sea resembles that of the northern part of the Gulf of California. Both lie in the same climatological region, but the Salton Sea is a relatively small and shallow body of water surrounded by desert (Carpelan, 1958). Consequently, its climate is even more extreme than that of the upper Gulf.

Dispersal

Pelagic larvae constitute the most likely avenues of genetic exchange between disjunct populations of *mirabilis*. The adults are closely restricted to their specialized and discontinuous habitats. At least some of the larvae must be swept out to sea where they could be distributed to other bays by the oceanic currents.

There is some evidence that the larvae of this genus are not adapted to a pelagic life as prolonged as those of the related genera, *Quietula, Clevelandia,* and *Ilypnus* (but not *Eucyclo-*

gobius). This conclusion is based on differences in postlarval pigmentation and behavior. Pelagic larvae and nektonic postlarvae characteristically are translucent with scattered melanophores, while the completely pigmented condition is found first in the benthonic stage. Postlarvae of *Gillichthys mirabilis* as small as 8–12 mm in length often are relatively heavily pigmented. At a comparable length, postlarvae of the other genera mentioned above are much more translucent.

Postlarvae of *mirabilis* in a slough in the northern Gulf of California, and at the Salton Sea, were seen to drift or swim into the current in slowly moving water. The postlarvae descended to the bottom and held station when the current strength increased. Postlarvae of *Quietula guaymasiae* Jenkins and Evermann were observed to form small groups that swam vigorously in a strong tidal current in the Gulf, darting from side to side at the surface in a manner reminiscent of young atherines; they seemed well adapted for life in open water. The larvae of *Gillichthys mirabilis* evidently are not dispersed as readily as are those of the related genera just mentioned.

Reproduction

Spawning apparently commences in January throughout the range of *mirabilis,* but the length of the season is uncertain. In southern California spawning takes place throughout the period from January to July (Weisel, 1947: 82). My observations indicate that spawning also starts in January in the Alviso ponds; females hatched there in January and February, however, are mature and full of ripe eggs in August and September of the same year. It is
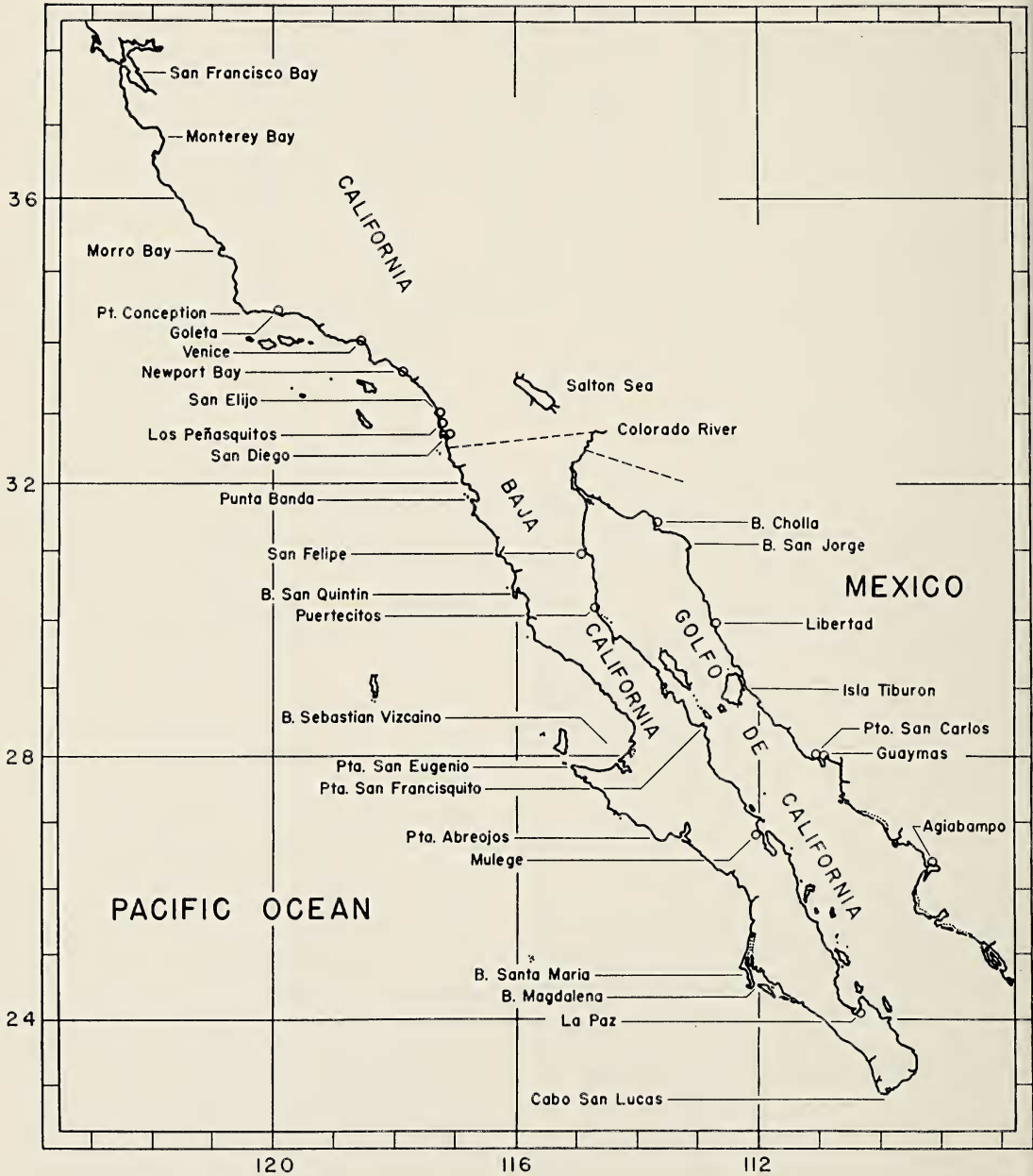
FIG. 1. Chart of the study region; latitude N, longitude W.

not known whether or not they spawn this late in the season. In the Salton Sea, the first spawning occurs in January and the last in May or June. Postlarvae of *mirabilis* have been collected in early February in the northern and central Gulf of California. There are no data available on the length of the spawning season in Gulf populations.

Depending on the size of the female, 4,000–9,000 eggs are laid at each spawning (Weisel, 1947: 80). Weisel believed that each female spawns once, rarely twice, in a season. Examination of ovaries of Salton Sea fish leads me to believe that each female *mirabilis* oviposits 2 or 3 times each season, with an interval of 40–50 days between spawnings. MacGinitie (1939: 500) reported that the related blind goby, *Typhlogobius californiensis* Steindachner, spawns twice during one season, with an interval of about 2 months. Females of a more distantly related goby, the mapo, *Bathygobius soporator* (C. and V.), can repeat a spawning in 7–16 days (Tavolga, 1954: 432). If the above estimates are correct, each female *Gillichthys mirabilis* has a potential production of about 8,000–27,000 eggs in one season.

The young of *mirabilis* reach maturity by the end of their first year. Rate of growth was investigated only at the Salton Sea. It is clear from these data and from the changes in size composition of collections from other locations taken at different times of the year, that most fish attain adulthood and a standard length of 100–140 mm by the end of their first year. Nothing is known of their life expectancy.

MATERIALS AND METHODS

In the preliminary analysis of *mirabilis* and *seta,* certain counts and measurements were selected as being especially promising (Barlow, 1961*a*). While investigating these, other useful characters also came to light.

All counts and measurements, except one, were carried out in accordance with the methods of Hubbs and Lagler (1949). The exception, the height of the anal fin, is defined here as the distance from the base of the last element of the anal fin to the tip of the second to last ray, when the fin is erect.

The study was based almost entirely on specimens deposited in the Fish Collections of the University of California, Los Angeles. About 4,000 specimens of *mirabilis* were examined. The fish from San Francisco Bay (Alviso ponds) were obtained from Sim's Bait Shop, Long Beach, California, and care was taken to verify the original source of this material. After fixation in 10% formalin, the specimens were washed and placed in 46% isopropyl alcohol.

Statistical Methods

The purpose of each statistical test in this paper is solely to accept or reject a hypothesis. The decision to accept or reject a hypothesis was based on the 5% critical level, to minimize type II errors (Hoel, 1954: 33). Acceptance of a hypothesis such as equal means, however, merely indicates no detectable differences and does not imply that the populations in question are proven to be the same. Critical values usually are given; the subscript notation 0.95 refers to a one-tail test, and 0.975 to a two-tail test.

Four kinds of tests were employed. The F-test was used when the hypothesis involved the testing of two variances. Covariance was applied to problems when two or more regressions (fitted by least squares) were tested at the same time. Decisions to accept or reject differences between two means were determined by *t*-tests. Correlation coefficients were evaluated as outlined by Hoel (1954: 124).

Obvious differences were not tested. When several variances or means were compared, the two most divergent values were examined first. If no significant differences were revealed, the others were not tested.

The statistical parameters of the fin ray counts are presented graphically. The format is that of Hubbs and Hubbs (1953). Unless the separation between means was patent, no statistical inferences have been drawn from these figures.

RESULTS

Head

The head of fish from the Gulf of California, as seen from the side, is more pointed than in Pacific Coast specimens. In this respect the Gulf populations approach *seta.* The difference in

TABLE 2

Fin Counts for *Gillichthys mirabilis*, Materials and Localities

°N	LOCALITY	COLLECTED	FIN COUNTS n (SIZE RANGE)
Pacific Coast			
37°27′	San Francisco Bay	June 1957	30(39–86)
35°20′	Morro Bay	August 1957	30(86–132)
34°24′	Goleta	September 1957	30(64–125)
34°00′	Venice	June 1957	28(83–138)
33°37′	Newport Bay	October 1955	25(56–154)
33°01′	San Elijo Lagoon	June 1956	30(58–142)
32°47′	Mission Bay	May 1946	30(38–54)
31°43′	Estero Punta Banda	July 1955, 1956	20(80–124)
30°30′	Bahia San Quintin	July 1956	14(91–142)
26°45′	Punta Abreojos	May 1948	16(10–20)
24°47′	Bahia Sta. Maria	April 1955	30(22–38)
Salton Sea			
33°18′	NW Shore	July 1953[1]	30(55–109)
	NE Shore	July 1954[1]	30(40–78)
	NW Shore	July 1955	30(35–74)
Gulf of California			
31°21′	Bahia Cholla	January 1949	30(20–30)
	Bahia Cholla	April 1954	30(48–88)
31°18′	San Felipe	April 1957	31(25–50)
27°57′	Estero Soldado	January 1952	31(15–20)
26°54′	Mulege	March 1957	30(35–50)
26°22′	Bahia Agiabampo	January 1951	10(66–100)

[1] Not included in Figures 6–12.

shape is due largely to the more depressed head of the Gulf fish, and was one of the main reasons for naming this form as a new species. In their description, Gilbert and Scofield (1898: 498) commented on the depressed head of *Gillichthys detrusus* (= *G. mirabilis* Cooper). This condition prevails in all the populations investigated from the Gulf. The mean head depth for fish from "El Marino" slough, just north of San Felipe, is 15.6% (13–18%; n = 10) of standard lenth, which agrees nicely with the value for Bahia Agiabampo fish (Barlow, 1961*a*). It should be noted at this point that the position of the opercles and the branchiostegals of preserved gobies can cause considerable variation in measurements of head depth and especially of head width.

The head shape of Salton Sea fish is more like that of specimens from the Pacific Coast than of those from the Gulf. The measured head depth, though, is closer to that of Gulf populations (Barlow, 1961*a*).

The regression of head length on standard length is slightly, but significantly, greater for the Pacific Coast populations than for the fishes from the Gulf when the data are pooled (Fig. 2, Table 3). Along the Pacific Coast the five populations also differ significantly from one another (Table 3). The differences between Gulf populations are of approximately the same degree as those between the Pacific Coast groups, but this was not tested statistically. Fish from the Salton Sea have the shortest heads, which is immediately noticeable when inspecting large adults.

Relative growth differences are seen best by plotting the logarithms of head and standard length (Martin, 1949: 8). The regressions for all populations so presented are nearly parallel (no figure). These curves for relative growth of the head, however, are slightly but clearly curvilinear; the slopes steepen with increasing standard length. The relative degree of difference between any of the lines is the same for the
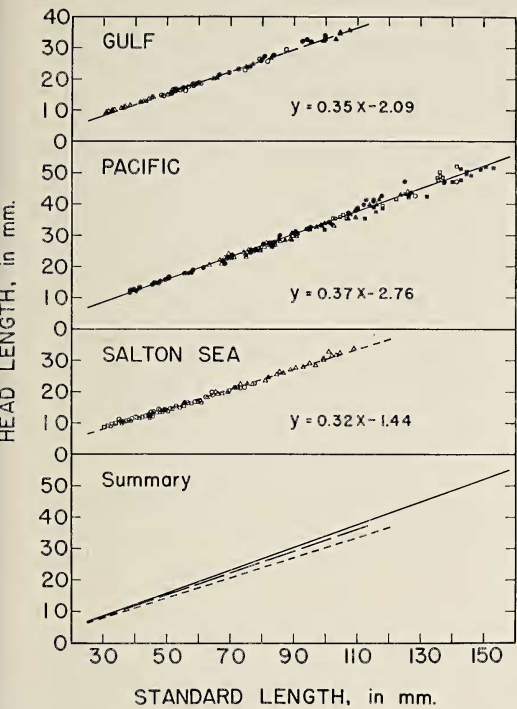
FIG. 2. Head length versus standard length. Gulf of California populations: open triangle, San Felipe (El Marino); open square, Mulege; open circle, Bahia Cholla, 1954; closed triangle, Guaymas (Estero Bocochibampo); closed circle, Agiabampo. Pacific Coast populations: closed circle, San Francisco Bay (Alviso ponds); open triangle, Goleta; closed square, Newport Bay; open circle, San Elijo Lagoon; closed triangle, Estero Punta Banda; open square, Bahia San Quintin. Salton Sea population: open triangle, 1953; open circle, 1954; open square, 1955.

smallest and largest fish measured, i. e., the lines are parallel. Therefore, differences between slopes of arithmetic plots presented here are of no biological significance.

Upper Jaw

The analysis of upper jaw measurements is complicated by the curvilinear relationship between jaw length and standard length. (Hereafter, upper jaw is referred to as jaw.) This difficulty is alleviated somewhat by fitting two regressions through the data: one line for fish greater than 90 mm, and another for the smaller specimens (Fig. 3). The change in slope is an artifact of the arithmetic plot; relative growth is only slightly curvilinear. The situation is also

complicated by the sexual dimorphism of jaw length in adult fish. The average length of the jaw is slightly greater in males, even though the range is about the same in both sexes. Consequently, the results of the covariance tests (Table 3) should be regarded with skepticism, since some of the assumptions underlying the test are not entirely satisfied.

The jaw of fish from the Gulf is about equal to, or slightly larger than, the jaw of Pacific Coast fish when specimens of the same length are compared. On the same basis, the jaw is much shorter in fish from the Salton Sea.

If jaw lengths are compared as a function of head length instead of standard length, the jaw is still relatively longest in Gulf fish and shortest
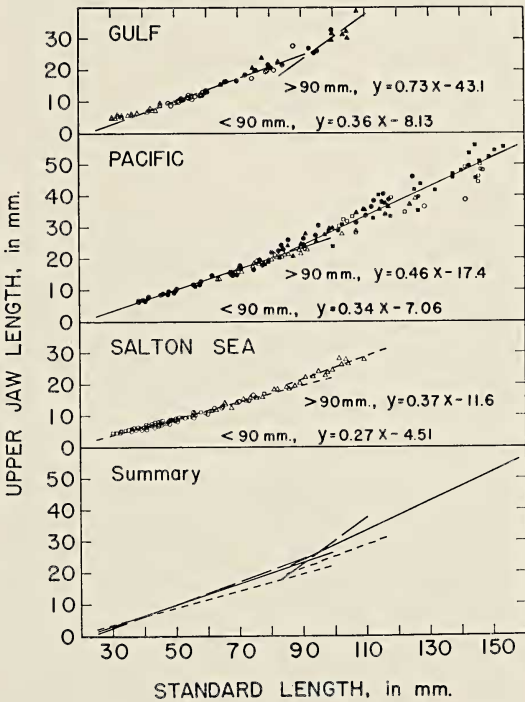

FIG. 3. Upper jaw length versus standard length. Gulf of California populations: open triangle, San Felipe (El Marino); open square, Mulege; open circle, Bahia Cholla, 1954; closed triangle, Guaymas (Estero Bocochibampo); closed circle, Agiabampo. Pacific Coast populations: closed circle, San Francisco Bay (Alviso ponds); open triangle, Goleta; closed square, Newport Bay; open circle, San Elijo Lagoon; closed triangle, Estero Punta Banda; open square, Bahia San Quintin. Salton Sea population: open triangle, 1953; open circle, 1954; open square, 1955.

TABLE 3

Results of Co-Variance Tests on Differences in Morphology of *Gillichthys mirabilis*
(Hypothesis tested is equal means after adjustment for standard length.
Key: F, F ratio; d.f., degrees of freedom; $F_{.95}$, 5% critical value.)

	F	d.f.	$F_{.95}$	DECISION
Head length				
Gulf/Pacific/Salton Sea	80.3	2,299	3.03	reject
Gulf/Pacific	8.87	1,201	3.89	reject
Pacific (5 populations)	14.8	4,128	2.44	reject
Salton Sea (1953–55)	10.1	2,97	3.09	reject
Salton Sea (1954–55)	3.36	1,66	3.99	accept
Upper jaw length				
> 90 mm				
Gulf/Pacific/Salton Sea	10.6	2,87	3.10	reject
< 90 mm				
Gulf/Pacific/Salton Sea	41.6	2,208	3.04	reject
Salton Sea (1953–55)	7.99	2,84	3.10	reject
Salton Sea (1954–55)	< 0.58	1,66	3.99	accept
Anal fin height				
Gulf/Pacific/Salton Sea	37.8	2,291	3.03	reject
Pacific (6 populations)	19.1	5,129	2.29	reject
Salton Sea (1953–55)	3.13	2,95	3.10	reject

in those from the Salton Sea. The jaw is 81, 74, and 71% of head length for Gulf, Pacific Coast, and Salton Sea fish, respectively. Thus, the jaw of the Salton Sea fish is shorter in regard to head length as well as standard length.

Median Fin Height

The soft dorsal and the anal fins are higher in fish from the Gulf than in those from California and the Salton Sea (Barlow, 1961*a*, table 1). Only the variation in anal fin height is reported in detail.

The anal fin height varies significantly from population to population along the Pacific Coast (Fig. 4, Table 3). San Francisco fish, for instance, often fall below the fitted regression; Newport Bay and Estero Punta Bunda specimens usually are above it. The data are too few to make an unequivocal statement about trends, but the fins of northern fish tend to be lower than those from the south.

Gilbert and Scofield (1898: 498) mentioned the higher anal fin of *detrusus* (= *mirabilis* Cooper) when they described it as a new species.

The type locality is the tidal region of the Colorado River delta, but high anal fins are also typical of the populations to the south in the Gulf (Fig. 4). The regression of fin length on standard length for Gulf forms is higher and steeper than those for the populations from the Pacific Coast and the Salton Sea. The variation between Gulf populations is assumed to be significant. No trend with latitude is apparent.

One sample from the northwestern region of the Gulf (an isolated salt pond 25 km north of San Felipe) has remarkably low median fins, and the dorsal fin profile is less rounded than in the typical Gulf form (Fig. 5). The height of the anal fin averages 8.8% (8.3–9.5%) of the standard length (based on 10 specimens, 61–102 mm in length). Thus the anal fin height and the dorsal fin shape resemble those of fish from the Pacific Coast. These data were not included in the regression of fin height versus standard length because the specimens had not been examined at the time the calculations were carried out and the figure was prepared. The fish of this population are thought to be not representative of the usual Gulf condition.
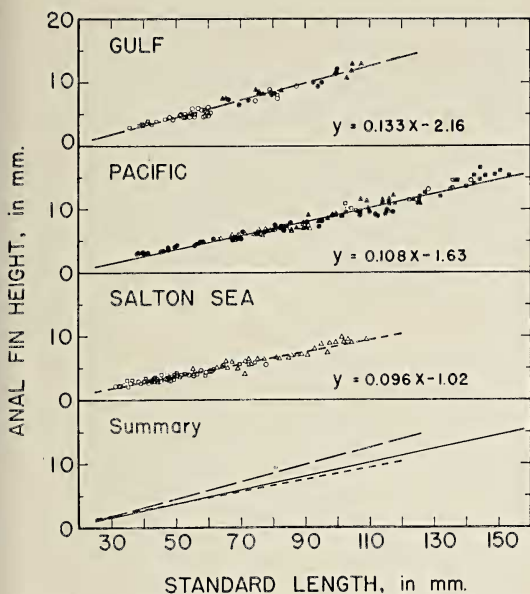
FIG. 4. Anal fin height versus standard length. Gulf of California populations: open triangle, San Felipe (El Marino); open square, Mulege; open circle, Bahia Cholla, 1954; closed triangle, Guaymas (Estero Boco-chibampo); closed circle, Agiabampo. Pacific Coast populations: closed circle, San Francisco Bay (Alviso ponds); open triangle, Goleta; closed square, Newport Bay; open circle, San Elijo Lagoon; closed triangle, Estero Punta Banda; open square, Bahia San Quintin. Salton Sea population: open triangle, 1953; open square, 1954; open circle, 1955.

The anal fin height of Salton Sea fish (Fig. 4) is considerably lower than in Gulf groups. Compared to Pacific Coast populations, the fin heights are similar but nevertheless lower. The variation in height from year to year in the Salton Sea fish is just significant at the 5% level.

The profile of the second dorsal fin is more rounded in specimens from the Gulf of California than in those from the outer coast or the Salton Sea. This results from the relatively greater increase in length of the centermost rays in the higher fins. Besides the change in shape, the anterior height of the second dorsal fin equals or exceeds that of the first dorsal in Gulf forms (Gilbert and Scofield, 1898: pl. 38). In fish from the Pacific Coast and the Salton Sea, the anterior rays are lower and the central rays are equal to or only slightly higher than the spiny dorsal.

Distance between Dorsal Fins

The distance between dorsal fins is greatest in fish from the northern part of the Gulf of California, ranging from 1.0 to 1.8 times the eye diameter. The distance between fins of specimens from the central and southern Gulf is about the same as that of fish from central California, being 0.7–1.1 times the eye diameter. The distance between dorsal fins was one of the diagnostic characters used by Gilbert and Scofield (1898: 498) to separate *detrusus* from *mirabilis*.

In Salton Sea fish, the distance between fins is less than one eye diameter. The posterior margin of the first dorsal sometimes touches the anterior margin of the second dorsal. A greater number of elements in both dorsal fins as well as an encroachment on the space by two to three supernumerary spines on the leading edge of the second dorsal fin cause the decrease in distance.

Squamation

The scales are slightly larger in specimens of *mirabilis* from the Gulf of California than they are in those from the outer coast and the Salton Sea. The counts range from 60 to 80 irregular vertical rows of scales along the body in Gulf forms, while there are about 80–100 rows in fish from the Pacific Coast and the Salton Sea.

The ventral squamation is more extensive in fish from the Gulf than in those from the Pacific Coast or the Salton Sea. The scales extend anteriorly around the base of the pelvic fin in about 30% of the specimens from Bahia Agiabampo (southern Gulf), in about 10% from Guaymas (central Gulf), and in about 80% from Bahia Cholla (northern Gulf). In fish from the Pacific Coast, the scales only occasionally reach anteriorly beyond the lateral insertion of the pelvic fin base.

In many respects the scalation is less extensive in Salton Sea fish, although the scales are about the same size as those on fish from the Pacific Coast. The ventral, anterior margin of the scaled area usually just reaches the insertion of the pelvic fins, but not beyond. The scaleless area directly under the pelvic fins is greater than in naturally occurring populations. The naked

area extends posteriorly to just beyond the tip of the pelvic fins but is not as wide as the pelvic fins; the size of the area is variable but is always larger than in other populations. A vertical strip in the axil, about one-half an eye diameter wide, is also without scales. Further, the strip of scales on the nape is shorter than in the other populations (Barlow, 1961a). The base of the caudal fin rays has two to six vertical rows of scales on it. In this respect only, the Salton Sea fish occasionally are more fully scaled than those of the other populations.

First Dorsal Fin

The average spine number is about six for all populations, although some means deviate appreciably from this value (Fig. 6). The count never was found to be less than six in Gulf populations. Five spines, however, are not uncommon in other populations. The only geographic trend discernible concerns the variances of the populations; this is reported below.

Second Dorsal Fin

The mean number of rays in the second dorsal fin is clearly higher in Pacific Coast than in Gulf populations (Fig. 6). On the Pacific Coast the counts are lower in the south, while in the Gulf the counts are more nearly uniform, or slightly higher in the south. Thus the average number of fin rays for Gulf and Pacific Coast

populations tends to converge in the lower latitudes.

The mean number of dorsal fin rays in the Salton Sea population is greater by about one ray than in the other populations.

The large range and variation of the Newport Bay population are caused chiefly by one specimen with only eight rays. The fin does not look aberrant but it must be considered atypical.

Anal Fin

On the Pacific Coast the mean number of anal fin rays increases from the north, south to San Diego, then decreases further south. In the Gulf, where samples are less complete, the means are about the same in all populations, or are a little higher in the south. The means of the Gulf and Pacific Coast populations converge in the lower latitudes (Fig. 7).

The mean number of anal fin rays in the fish from the Salton Sea is conspicuously higher than in any of the naturally occurring populations (Fig. 7).

Pectoral Fin

The mean number of pectoral fin rays increases progressively from north to south on the Pacific Coast, but in the Gulf of California the average number decreases to the south. Consequently, the means of Pacific Coast and Gulf
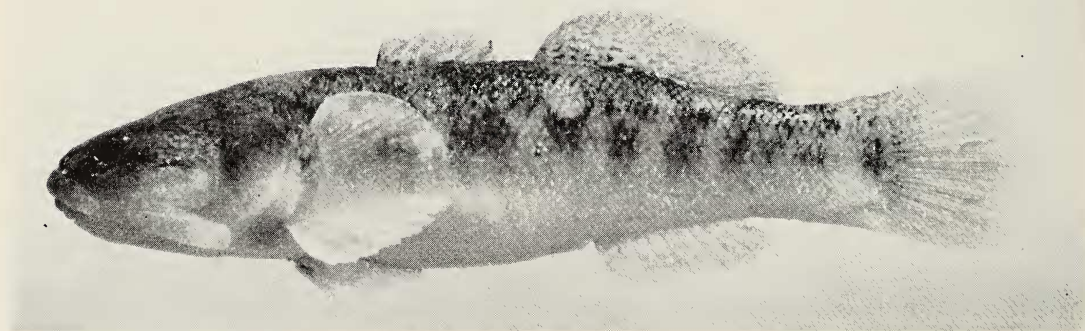

FIG. 5. *Gillichthys mirabilis,* female, standard length 100 mm, from "El Marino" slough north of San Felipe, Baja California. The small black spot on the side of the specimen is a blemish.
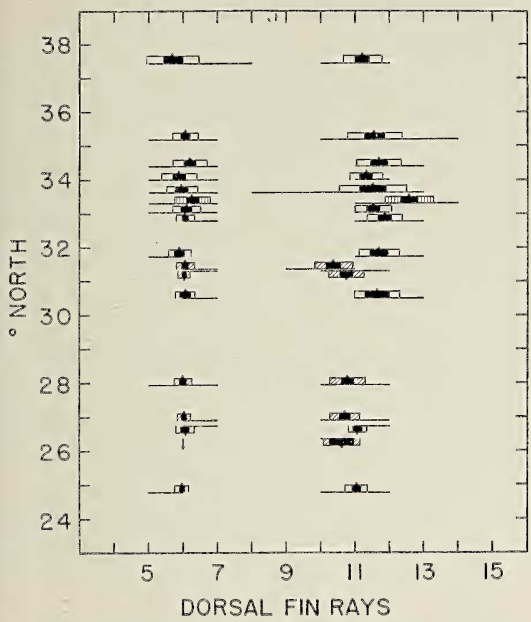
FIG. 6. Fin rays in the first (spiny) and second (segmented only) dorsal fins, from left to right, presented as a function of °N latitude. Materials and place names in Table 2. Large rectangle, one standard deviation on either side of mean (triangular prominence); blackened space, two standard errors on either side of mean; lower horizontal line, range of counts. Open rectangle, Pacific Coast populations; vertical lines in rectangle, Salton Sea population; oblique lines in rectangle, Gulf of California populations.

populations overlap in the southern latitudes (Fig. 8).

The average pectoral fin count of the Salton Sea fish again is much higher than in Pacific Coast animals. The number of fin rays, however, is similar to that found in northern Gulf populations (Fig. 8).

The Venice population, near Los Angeles on the Pacific Coast, is extremely variable. Some pectoral fins are deformed and obviously are aberrant. This habitat is polluted by sewage and industrial waste products.

Combined Fin Counts

Some of the trends and differences observed in the study of individual fins disappear when the fin counts are combined and plotted as a function of latitude (Fig. 9). At different latitudes the averages of the combined fin counts

are about the same, except in California where a slight increase from north to south occurs. Otherwise there is no trend in the mean number with latitude. When comparisons are made at the same latitudes, the Pacific Coast populations and all of the Gulf populations, except for San Felipe, broadly overlap. Contrariwise, some divergences are enhanced. The Salton Sea and San Felipe populations are obvious deviants. Further discussion of combined fin elements is reserved for the section on annual variation.

Fin Ray Variance

Over the geographic range of *mirabilis* there are dissimilarities in the variances of each of the fins. The difference between the extreme variances of the first dorsal fin on the Pacific

FIG. 7. Fin rays in the anal fin (segmented only) presented as a function of °N latitude. Materials and place names in Table 2. Large rectangle, one standard deviation on either side of mean (triangular prominence); blackened space, two standard errors on either side of mean; lower horizontal line, range of counts. Open rectangle, Pacific Coast populations; vertical lines in rectangle, Salton Sea population; oblique lines in rectangle, Gulf of California populations.
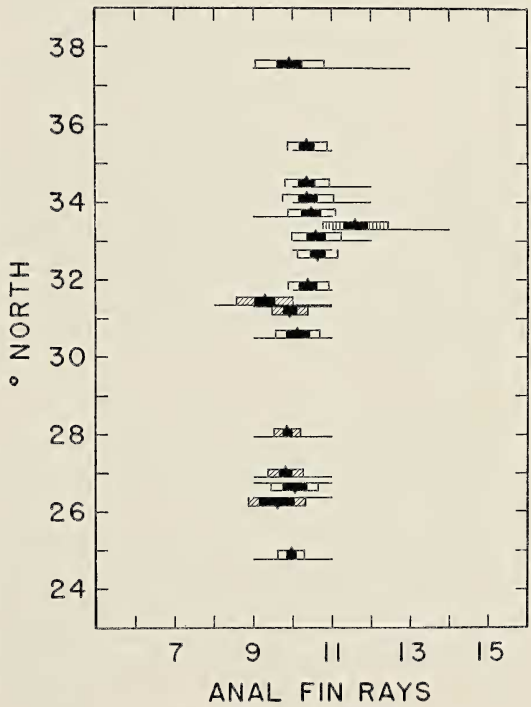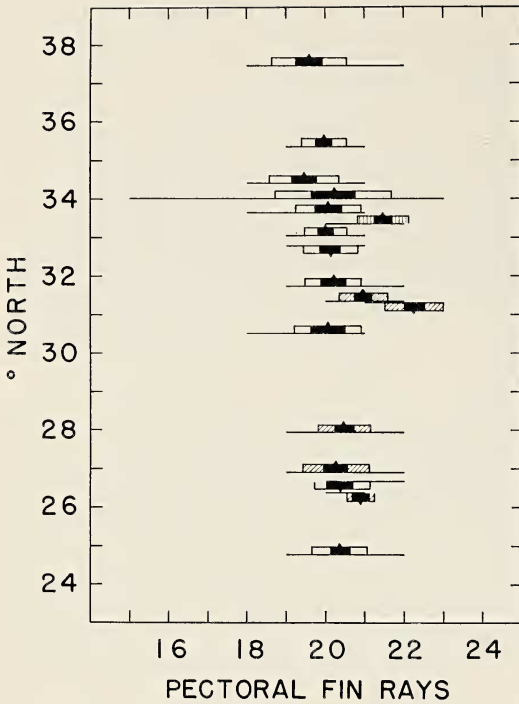
FIG. 8. Fin rays in the left pectoral fin presented as a function of °N latitude. Materials and place names in Table 2. Large rectangle, one standard deviation on either side of mean (triangular prominence); blackened space, two standard errors on either side of mean; lower horizontal line, range of counts. Open rectangle, Pacific Coast populations; vertical lines in rectangle, Salton Sea population; oblique lines in rectangle, Gulf of California populations.

between latitude and variance of the vertebrae (see below).

The correlation between degrees of latitude and variance of the first dorsal fin has a coefficient of 0.848, which differs significantly from a coefficient of zero. This high degree of correlation doubtless could be increased further by reducing that portion of the intra-population variation resulting from sampling techniques, thereby improving the estimate of the real variance. As will be seen further on, comparisons of relatively homogeneous year classes from succeeding years show that even though the mean number of elements in the various fins may change, the variance remains the same. Some

Coast (San Francisco Bay and Bahia Santa Maria), for instance, is highly significant: $F = 16.9$, $F_{0.975}$ (29, 29) $= 2.1$.

The intrinsic variability in the number of elements in a given fin is associated with the latitude where the population is situated. Increasing variability is associated with higher latitudes (Fig. 10). All the fins manifest this increase in variability from south to north, though not equally well. If one were to rate the correlations subjectively from good to poor, they would stand in the order (1) first and second dorsal fins, (2) combined counts, (3) anal fin, and (4) pectoral fin. Only the data from the first dorsal fin are presented here (Fig. 10); the other data are available on request. There also may be a positive correlation

FIG. 9. Combined elements, segmented and unsegmented, in the first and second dorsal, anal, and left and right pectoral fins, presented as a function of °N latitude. Materials and place names in Table 2. Large rectangle, one standard deviation on either side of mean (triangular prominence); blackened space, two standard errors on either side of mean; lower horizontal line, range of counts. Open rectangle, Pacific Coast populations; vertical lines in rectangle, Salton Sea population; oblique lines in rectangle, Gulf of California populations.

FIG. 10. Correlation between population variances (±) of the first dorsal fin, and °N latitude. Open circle, Pacific Coast populations; closed triangle, Salton Sea population; closed circle, Gulf of California populations.

of the samples represented by a single value in Figure 10 are heterogeneous, consisting of more than one year class. Similar dispersion in each year class, but about different means, would increase the apparent variation.

Fin Ray Correlations
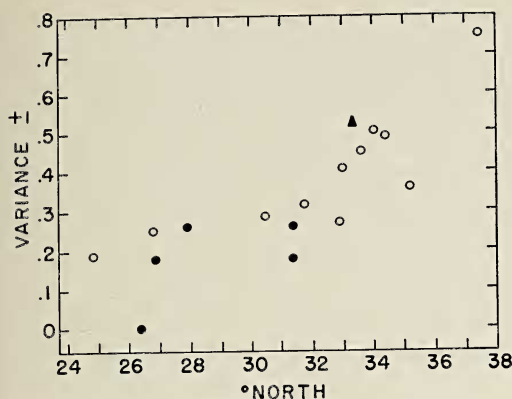
The segmented rays of the dorsal and anal fins are positively correlated. When all the counts are combined, exclusive of the Salton Sea, the correlation coefficient is 0.603, significantly greater than zero. A positive correlation also is evident within and between year classes.

The number of elements in the pectoral fin compared to that of the anal, and of the soft dorsal fin, reveals negative correlations, but only when means of different populations are compared (Fig. 11). The correlation coefficient for the pectoral fin with the second dorsal fin is −0.737, and with the anal fin it is −0.659; both values differ significantly from zero. The data for the sample from San Felipe are shown in Figure 11 (the highest pectoral fin mean) but are not included in the computations of the correlation coefficients; as mentioned before, the counts are atypical. The inclusion of these counts does not affect the conclusion that the pectoral and median fin counts are significantly correlated. Data from samples from the Salton Sea also are not included.
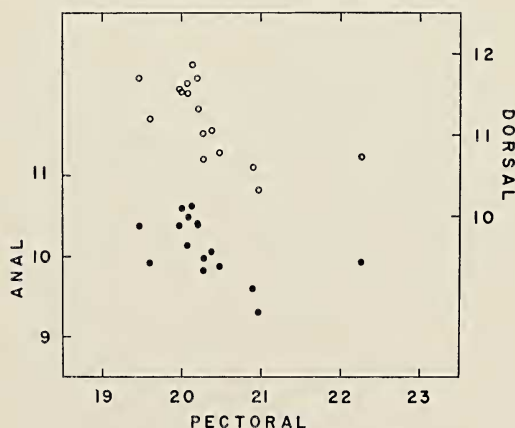
Fin Ray Index

Probably the most useful statistic obtained from the fin counts is a derived index. The soft rays of the dorsal and anal fins are summed, then divided by the number of rays in the left pectoral fin and multiplied by 100. This index reflects the change in relationship between the fin ray numbers of pectoral and median fins at different latitudes (Fig. 12).

On the Pacific Coast, not including San Francisco and Venice, the index decreases progressively from north to south. In the Gulf of California the opposite is the case; the index increases to the south. The indices of Gulf and outer-coast populations consequently converge at low latitudes, being slightly higher in outer-coast populations.

Noteworthy is the excellent agreement of index values for samples from Bahia Cholla and San Felipe, situated at similar latitudes but on opposite coasts of the Gulf. This is especially striking, considering that the San Felipe fish have unusually high atypical counts.

The most revealing index is that of the Salton Sea population. It agrees with values obtained from samples taken in the vicinity of San Diego, the source of the Salton Sea stock. Further, the index is considerably higher than in any of the Gulf populations.

FIG. 11. Correlation between population means of number of pectoral fin rays, and number of segmented rays in the anal (closed circles) and dorsal (open circles) fins.
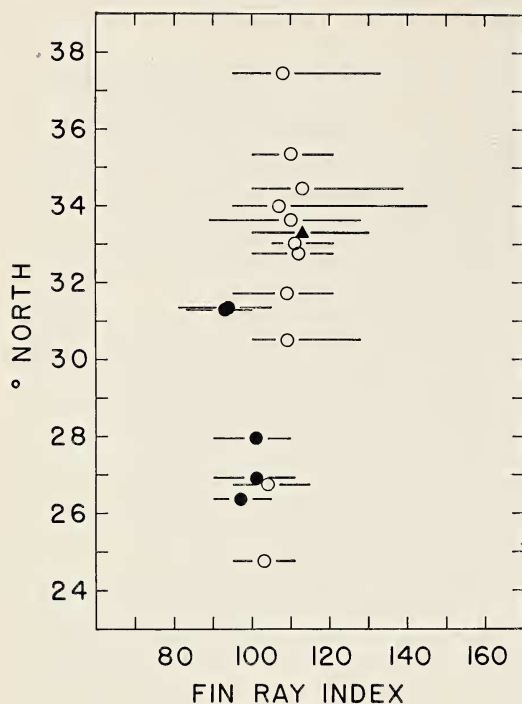
FIG. 12. Fin ray index: combined number of segmented rays in the second dorsal fin and anal fin, divided by the number of rays in the left pectoral fin, multiplied by 100. Open circles, means of Pacific Coast populations; closed circles, means of Gulf of California populations; closed triangle, mean of Salton Sea population; horizontal lines, ranges of values.

Pectoral Fin Asymmetry

Species of fishes are known to differ in degree of asymmetry between the number of elements in the right and left pectoral fins (Hubbs and Hubbs, 1945). The numerical asymmetry between right and left pectoral fin counts in *mirabilis* was investigated to determine if individual populations, or geographic regions, could be characterized by this feature (Table 4). Only the total amount of asymmetry, right plus left, was found to be useful in this respect. Values for the Pacific Coast and Salton Sea populations are usually higher (mean about 30%) than those from the Gulf (mean about 20%). The amount of asymmetry in the two most southerly populations on the Pacific Coast, however, is the same as that of the Gulf forms.

The degree of asymmetry is equally divided between right and left. To facilitate comparisons, each population can be characterized according to whether there are more fish with higher counts in the right fin than in the left fin, or vice versa. If a sample has more fish with right fins of a higher count than the left, it is tallied as a "dextral"; and with more lefts than rights, as a "sinistral."

Among collections from the Pacific Coast 5 out of 11 are dextral. In the Gulf, 3 out of 6 are dextral, 1 is sinistral, and 2 are equal. The Salton Sea population vacillates from year to year between dextral and sinistral. Therefore, the distribution of rights and lefts within and between populations is typical of a 50–50 chance situation, such as the toss of a coin.

Vertebrae

The number of vertebrae was compared in five populations (Table 5). In every sample the mode is 32, and the average is approximately the same value. Only the mean of the Salton Sea specimens differs appreciably from 32; it is significantly higher ($t = 2.02$; $t_{0.95}$ (29) = 1.70).

In contrast to the relative uniformity of the means, there are patent differences between the variances; they are greater in the Salton Sea and Pacific Coast groups than in those from the Gulf. Each of the variances of the San Francisco and Salton Sea samples was tested against that of the northern Gulf collection; the F–ratios are F = 13.6, $F_{0.975}$ (18, 39) = 2.4, and F = 8.6, $F_{0.975}$ (29, 39) = 2.1, respectively. The variances of the San Francisco and Salton Sea groups are not significantly different: F = 1.6, $F_{0.975}$ (18, 29) = 2.5.

The variances of the vertebrae decrease from high to low latitudes. If the variances are listed from north to south, instead of as shown in Table 5, the following series of values is obtained: 0.577, 0.461, 0.182, 0.157, 0.341, 0.0. Considering the few populations represented, the correlation is surprisingly good. The presence of a similar positive correlation between latitude and fin ray variance (see above) increases the confidence in the trend indicated by the variances of the vertebrae.

Annual Variation

Material for the study of annual variation came from the Salton Sea and from Bahia Cholla (northern Gulf of California). Each sample was from a year class hatched in the year considered. This affords a rough estimate of the stability of the statistical parameters used in the comparison of separate populations.

The Salton Sea was sampled during the same month on three successive years. The fish of one sample are larger than the others (Table 6) and probably were hatched earlier in the year than those of the other two samples. In addition, the 1954 collection was from a different part of the Sea, but I doubt that this is of importance. Both body measurements and fin counts were taken.

The two samples from Bahia Cholla came from year classes that had hatched under strikingly different temperature conditions. The first were embryos during an unusually cold period late in the winter of 1949. A moderate fish kill occurred in the northern Gulf at that time. The second collection, 1954, consists of fish that had developed in a relatively normal temperature situation. Only counts were taken because the specimens are small.

Slight, but significant, differences occur between the means of fin counts of different year classes from the Salton Sea (Table 6). In the 1955 class, all counts are higher than in the previous two years (except for the first dorsal fin: 1955 vs. 1953, $t = 0.67$, $t_{0.95} (58) = 1.67$). The mean of the second dorsal fin exceeds that of the anal fin by about one ray in each year class.

The ratios of median fin rays to pectoral rays, as indicated by the fin indices, remain approximately the same. Thus while the means

TABLE 4

BILATERAL ASYMMETRY OF PECTORAL FINS
ARRANGED BY REGIONS, FROM NORTH TO SOUTH

AREA	n	PERCENTAGES		
		L > R	R > L	R + L
Pacific Coast				
San Francisco	30	17	20	37
Morro Bay	30	23	10	33
Goleta	30	10	27	37
Venice[1]	28	29	25	54
Newport Bay	25	4	12	16
San Elijo Lagoon	30	13	23	36
Mission Bay	30	3	13	16
Estero Pta. Banda	20	25	10	35
Bahia San Quintin	14	14	21	35
Pta. Abreojos	16	19	6	25
Bahia Sta. Maria	30	13	3	16
Salton Sea				
1953	30	17	13	30
1954	30	7	10	17
1955	30	20	13	33
Gulf of California				
Bahia Cholla—1949	30	10	17	27
Bahia Cholla—1954	30	10	10	20
San Felipe	31	10	3	13
Estero Soldado	31	13	16	29
Mulege	30	10	10	20
Bahia Agiabampo	10	0	10	10

[1] Aberrant; see pectoral fin section.

TABLE 5

VERTEBRAL COUNTS FOR *Gillichthys mirabilis*
(Key: x, mean; s, one standard deviation.)

AREA	YEAR	NO. OF VERTEBRAE			STATISTICAL PARAMETERS		
		31	32	33	n	x	±s
Pacific Coast							
San Francisco	1955	3	13	3	19	32.00	0.577
Pta. Abreojos	1948	2	14	1	16	31.88	0.341
Gulf of California							
Bahia Cholla	1949	–	29	1	30	32.03	0.182
San Felipe	1955	–	39	1	40	32.03	0.157
Est. Soldado	1952	–	30	–	30	32.00	0
Salton Sea	1955	1	23	6	30	32.17	0.461

of fin ray counts may change, the relationships between them are relatively unaffected.

The divergence of means between the year class samples from Bahia Cholla is greater than that recorded in the Salton Sea material. The mean number of rays for each fin, except the first dorsal, is higher in the "cold" year than in the "normal" year fish. The differences are significant at the 5% critical level. The outstanding deviation is in the mean of the second dorsal fin which is higher by one full ray.

The relationship between the counts of the fin rays also is different in the 1949, or "cold" year class from Bahia Cholla. This results from the disproportionate increase of the soft dorsal fin count, which exceeds the anal fin by 1.7 rays. In most populations, as in the 1954 collection from Bahia Cholla, the average number of rays in the second dorsal fin surpasses that in the anal by only about one ray (0.8 to 1.3).

The fin index also reflects the change in the relationship between the fin counts. It is higher by 4% in the 1949 sample, probably due to the unusual rise in the number of dorsal fin rays.

Although the average number of fin rays and their interactions may change from year to year, the variance of each fin remains the same. F–tests were performed using the maximum and minimum variance of each fin within the year classes of each population; all F-ratios were below the 5% level of significance.

The direction of the annual variation in fin counts is of particular importance to conclusions drawn later. In each instance when a year class deviates to a noticeable degree, the direction of the changes are the same for all fins with segmented rays. Increases in the dorsal and anal fin counts, as just shown, are paralleled by an increase in the number of pectoral fin rays; i. e., they are positively correlated. Within any one year class, however, there is no correlation whatsoever between the number of segmented rays in median fins and in the pectoral fins (Table 7). The pectoral fin counts are the same, on the average, whether a fish has many or few median fin rays, when from the same year class.

The bilateral asymmetry of the number of pectoral fin rays fluctuates between samples of year classes from the Salton Sea and from Bahia Cholla. Both the amount and the direction of the asymmetry vary (Table 4). The total asymmetry is maximal in the Salton Sea sample for 1955 and in the Bahia Cholla collection taken in 1949.

The head and jaw length and the anal fin heights are about the same in the three year classes collected from the Salton Sea. When the three groups are tested together, the differences are significant (Table 2), although the comparison of anal fin heights for all three samples just exceeds the 5% level of significance. If only the 1954 and 1955 samples are compared, the differences no longer are significant (Table 3). The size ranges of the 1954 and 1955 samples nearly coincide, while that from the 1953 year class contains larger fish. The inclusion in

the test of the sample with the larger fish apparently causes the significant differences between the groups. Hence the differences between the three year classes seem to be caused by unequal size groups.

Peculiarities of G. mirabilis *from the Salton Sea*

The *mirabilis* introduced into the Salton Sea differ from naturally occurring populations in several ways. Most of these differences seem to indicate an interference with the normal developmental physiology.

Some of the unusual features of the Salton Sea fish have already been discussed in earlier sections, and they are enumerated below. All the counts of fin rays and vertebrae are higher in these fish than in any others. The relationship between the fin ray numbers as reflected by the fin index, however, has remained the same as that of the parental stock. The squamation is

less extensive, and the head and upper jaw are disproportionately small. The formation of the interorbital pore is delayed.

The Salton Sea fish differ from naturally occurring forms in still other ways not yet described. The otoliths are much coarser and more opaque than those of specimens from the outer coast. The outline of the otoliths, as seen from either flat side, is less angular and is often almost round. The edges of the otoliths usually are only weakly crenulate or smooth, and the characteristic notch is indistinct.

In gobiid fishes, the segmented rays of the soft dorsal and anal fin typically are preceded by one slender spine. This holds for *mirabilis* in naturally occurring populations, with rare exceptions. Supernumerary spines, however, have been found on two specimens of *mirabilis* from San Elijo Lagoon and one from Newport Bay, and also on one specimen of *seta* from San

TABLE 6

Annual Variation of Fin Counts of *Gillichthys mirabilis*
(Key: x, mean; s, one standard deviation; r, range.)

	SALTON SEA			GULF OF CALIFORNIA	
COLLECTED	NW Shore 18 July 1953	NE Shore 17 July 1954	NW Shore 13 July 1955	Bahia Cholla 27 January 1949	Bahia Cholla 27 April 1954
Size range in mm	55–109	40–78	35–74	20–30	48–82
n	30	30	30	30	30
First dorsal					
x	6.23	6.27	6.27	6.07	6.07
±s	0.504	0.451	0.521	0.255	0.253
r	(5–7)	(6–7)	(5–7)	(6–7)	(6–7)
Second dorsal					
x	12.43	12.33	12.57	11.33	10.37
±s	0.679	0.547	0.679	0.480	0.555
r	(11–14)	(12–14)	(11–14)	(11–12)	(9–11)
Anal					
x	11.27	11.33	11.60	9.60	9.30
±s	0.583	0.480	0.814	0.564	0.702
r	(10–12)	(11–12)	(11–14)	(9–11)	(8–11)
Pectoral (left)					
x	21.33	21.33	21.47	21.30	20.97
±s	0.679	0.480	0.628	0.625	0.616
r	(20–23)	(21–22)	(20–22)	(20–23)	(20–22)
Combined					
x	74.93	74.67	75.70	71.73	69.67
±s	1.68	1.18	1.95	1.53	1.65
r	(72–79)	(73–77)	(71–80)	(69–76)	(66–72)
Index					
x	112	111	113	98	94

TABLE 7

RELATIONSHIP BETWEEN THE PECTORAL FIN RAYS AND THE SUM OF THE SEGMENTED RAYS OF THE SECOND DORSAL FIN AND ANAL FIN IN *Gillichthys mirabilis*

DORSAL PLUS ANAL SEGMENTED RAYS	17	18	19	20	21	22	23	24	25	26	27
San Elijo Lagoon											
mean pectoral rays					20.0	20.0	20.0	20.0			
(n)					(9)	(10)	(9)	(2)			
Salton Sea											
1953											
mean pectoral rays							21.0	21.1	21.2	21.7	21.0
(n)							(2)	(11)	(9)	(6)	(2)
1954											
mean pectoral rays								21.5	21.1	21.2	
(n)								(17)	(8)	(6)	
1955											
mean pectoral rays						22.0	21.5	21.3	21.5	21.0	22.0
(n)						(1)	(11)	(6)	(8)	(2)	(2)
Bahia Cholla											
mean pectoral rays	21.0	20.0	21.0	21.0	21.0						
(n)	(1)	(1)	(10)	(15)	(3)						

Felipe. But in fish from the Salton Sea, the segmented rays of each of these fins are commonly preceded by two, or occasionally three, spines. When two spines are present in the soft dorsal or anal, the anterior-most spine is short. Usually it is less than one-half the length of the first segmented ray. Sometimes it is difficult to find the anterior-most supernumerary spine. In the soft dorsal only, the first of three spines is always short (usually a stub) and sometimes does not reach through the skin, while the second usually is moderately well developed and may be greater than half the length of the first segmented ray.

Supernumerary spines occur in the second dorsal fin more often than in the anal fin. In samples from 3 successive years (in each, n = 30), the percentages of the fins with extra spines are: second dorsal = 40, 13, and 33; anal = 10, 3, and 3. These data are from direct observations.

Photographs with X-rays revealed the presence of additional spines beneath the skin and of their basal elements. In one collection (n = 30, from 1955, but a different sample than the one mentioned in the preceding paragraph),

53% of the specimens have two spines in the soft dorsal and 10% have three (total = 63%). In the same sample, 13% of the fish have two spines in the anal fin, but none have three.

The situation is further complicated in that the number of spines does not always agree with the number of basals. Three specimens with only one spine in the fin have two basal elements. There is an additional basal anterior to the basal of the first, and only, spine. In two specimens, on the other hand, two spines share a single basal. In these cases, the first spine is merely a stub. In the specimens with three spines, three basals are found. Generally, elements are added anteriorly onto the anal fin, and especially the soft dorsal fin. This is done either by adding spines, basal elements, or both.

Axial deformities are conspicuous in fish from the Salton Sea (Fig. 13). Mostly they are situated anterior to the origin of the second dorsal fin. These are predominantly direct dorsal flexures, but may tend to right or left. Posterior to the first dorsal fin, the flexures are divided about equally between dorsal, lateral, and ventral. A few specimens have severe lateral flexures in the hypural plate (Fig. 13). More than one

flexure per fish is not uncommon. Photographs with X-rays indicate that the structure of the vertebrae has broken down at the apex of the more extreme curvatures. Whether there is a disintegration and/or fusion of the vertebrae is not clear from the photographs.

The occurrence of axial deformities increases during the hottest months of the year (Table 8). During July, the incidence of twisted specimens increases from around the usual 25% to 30%. The maximum occurs in the period of October to December. (The very high value for October is based on a small sample and therefore is subject to greater errors of random sampling. There is also a serious problem in obtaining a truly random sample, because of the sudden appearance of deformities in the young fish.)

Axial aberrations usually are manifest for the first time in subadults during August, the peak of the hot season. There is no relationship between size and incidence of deformities in these young fish. The deformities appear during the same period of time but not at a given size.

Axial deformities are also apparent in the sciaenid fishes that have been introduced into the Salton Sea. Here, too, anterior kyphosis seems to be prevalent.

Other abnormalities are seen in *mirabilis* but are not as common as the axial terata. These include forward projection of the lower jaw (Fig. 13), dermal flaps on the upper jaw, and pronounced elongation of individual rays in the median fins.

DISCUSSION

Body Form

Differences in size and shape are apparent in comparisons between various kinds of fishes from waters of different temperatures. Almost invariably in the Northern Hemisphere, the more northern representatives of a species or of a genus are larger than those to the south (Hubbs, 1926: 60; Vladykov, 1934: 120). The changes in body proportions have not been as thoroughly investigated, but some tentative generalizations can be made. Northern, slowly growing races of a species usually have smaller heads, eyes, maxillas, and fins than do their southern counterparts, although opposite effects are not uncommon (Hubbs, 1926: 62; Vladykov, 1934: 118; Martin, 1949: 23; and included references).

Morphological differences in *Gillichthys mirabilis,* as indicated by lines fitted to part lengths versus standard length, are apparent between the aggregates of populations from the Gulf of California and the Pacific Coast, and between the populations within these regions. There is no pattern among the regressions (length of parts on standard length) which might provide a clue to the nature of the differences. There is only the slightest tendency for the height of the anal fin to be greater in more southern populations of the Pacific Coast region.

The Gulf populations differ, for the most part, from those on the outer coast in the way one would predict for faster developing fish.
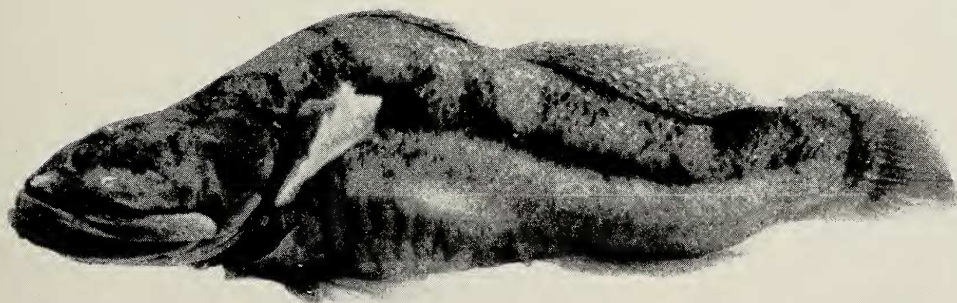

FIG. 13. *Gillichthys mirabilis,* female, standard length 101 mm, from the Salton Sea, California, and typical of extreme terata. Fold below the pectoral fin is from an incision.

TABLE 8

AXIAL DEFORMITIES IN *Gillichthys mirabilis*
FROM SALTON SEA

MONTH	TOTAL FISH	DEFORMED FISH	PERCENT DEFORMED
1955			
April	19	5	26
May	98	26	27
June	124	34	27
July	37	11	30
August	45	14	31
October	15	8	53
December	98	36	37
1956			
January	136	33	24
February	32	8	25

The Gulf fish have higher fins and longer jaws, the head is more depressed, and they tend to be more completely scaled ventrally and have slightly larger scales. The head is shorter, however. Except for the slightly shorter head length, the form of *mirabilis* from the Gulf is consistent with a hypothesis of rapid development. As seen in the fish from the Salton Sea, shorter head length is correlated with lower fins, shorter jaws, and reduced scalation, and presumably this has resulted from retarded development. If, as suggested, the Gulf fish differ morphologically because of faster development, then they should have longer, not shorter, heads. This contradiction probably stems from genetic differences.

No satisfactory explanation can be given for the distinctly greater distance between dorsal fins of the specimens of *mirabilis* from the upper Gulf as compared with the other populations. The form of the fish from the upper Gulf, however, resembles that of fish from the lower Gulf, except for the distance between dorsal fins. Environmentally induced changes usually manifest themselves in several ways, instead of being expressed in one character only. The increased space between dorsal fins, therefore, most likely has a genetic basis.

Countable characters

One of the commonly accepted generalizations in ichthyology is that the number of elements in serially repeated characters tends to be greater at higher latitudes (Vladykov, 1934: 102). Hubbs (1922, 1926) argued that this relationship depends chiefly on the temperature of the water during early development; lower temperatures were thought to result in increasing numbers of elements, and higher temperatures in lower numbers. Local temperature conditions have been observed to be associated with the anticipated changes in counts (reviewed in Barlow, 1961*b*). Moreover, any factor of the environment affecting rate of development, such as salinity or oxygen tension, seems to have effects similar to those thought to be produced by the thermal regime (Hubbs, 1926; Tåning, 1952; Seymour, 1956).

There are exceptions, however, where the change in counts goes contrary to expectations. In certain instances (Schmidt, 1919: 148; Hubbs, 1921: 150; 1924; Schultz, 1927: 420) the counts from one fin only showed an increase associated with warmer temperatures. The other fins manifested the normal negative correlation between number of elements and water temperature.

In spite of laboratory findings that the relationship between meristic structures and developmental temperatures is exceedingly complex, the pattern in natural populations of the same species is usually straightforward: higher temperatures during development normally bring about lower counts (Barlow, 1961*b*).

At first glance the changes in countable characters over the geographic range of *mirabilis* seem to indicate a gradient resulting from direct modification by the environment. Presumably, factors which cause a decrease in the dorsal and anal fin counts conversely bring about an increase in the number of pectoral fin rays.

Geographically, then, the number of median fin rays is negatively correlated with the number of pectoral fin rays. Johnsen (1936: 8–9) reported the same relationship between fins for various populations of *Gobius flavescens* and *Gobius minutus*. These changes could be construed as the result of dissimilar water temperatures or some related factors.

It is more probable, nonetheless, that the cline in meristic characters results primarily from different genotypes, not exclusively from environmental modification. This hypothesis can

be supported by more than one line of evidence.

The gradient of meristic characters in *mirabilis* follows the temperature gradient of the late summer period. The number of rays in the dorsal and anal fins increases from north to south in the Gulf of California, whereas over the same latitude on the Pacific Coast the opposite relation holds, and the counts tend to decrease from north to south. The same reversal of trends between the Gulf and outer coast occurs in the pectoral fin.

The fin indices decrease from north to south on the Pacific Coast, but continue to decrease in the Gulf from south to north. Thus a continuous cline in the meristic characters exists from San Francisco south, on the Pacific Coast, and then north up into the Gulf of California.

It might be argued that the late summer temperature gradient in the Gulf is opposite to that of the outer coast, and that this environmenal difference directly accounts for the reversal of the fin-index gradient. This cannot be the case, because the counts are determined while the eggs and larvae develop during late winter through early summer; then the temperature gradients of the Gulf and Pacific Coast are parallel, warmer to the south. If any correlation exists between environmental temperatures and number of countable elements, it is with the gradient of extremely warm temperatures found late in the summer, not those occurring during early development.

This cline, however, might reflect nothing more than the progressive physical separation between populations.

The fin index for *seta* in the upper Gulf of California continues the trend noted in *mirabilis,* that is, for lower indices toward the north in the Gulf. The average value for *seta* there is about 82 as compared to about 95 for adjacent populations of *mirabilis*. The temperature situation that prevails in the habitat of *seta* could be regarded as an extension of the gradient seen in the habitats of *mirabilis* from south to north in the Gulf. The habitat of *seta* is located on the coast in the high intertidal zone among black lava flows, boulders, and streams of seepage water (Barlow, 1961*a*). Climatically this environment is even more rigorous, and surely experiences higher summer temperatures than do the nearby sloughs where *mirabilis* occurs.

Returning to the fin indices of *mirabilis,* specimens from the Salton Sea, compared to their parental stock, have much higher counts in their dorsal and anal fins, and in their pectoral fins as well. The differences probably can be attributed to retardation of developmental rate. If the interaction between these fins behaved as expected from observations on the geographical cline, the pectoral fin counts should have decreased while the median fin counts increased. As shown by the fin index, the relationship between median and paired fins, remarkably, is unchanged in these fish.

Fluctuations in the mean number of segmented rays from year to year in a given population are in the same direction for the median fins and the pectoral fins. In other words, the changes in the number of elements in paired and median fins are positively correlated in their response to environmental changes. Colder years induce the formation of more rays in all of these fins.

In each fish, however, the number of pectoral fin rays appears to be inherited independently from the number of median fin rays. In a given year class, the fish with more numerous rays in the median fins have, on the average, the same number of pectoral fin rays as do fish with less median fin rays. Thus the median fin and the pectoral fin elements respond to the environment in the same way, but independently of each other.

From the foregoing evidence it seems reasonable to conclude that the change in relationship between the number of elements in the median fins and in the pectoral fin, the fin index, over the geographic range of *mirabilis* indicates genetic divergence.

Analogous differences between inter- and intra-populational variation have been observed in other gobies (Johnsen, 1936: 8–9). In different populations of *Gobius flavescens* and *G. minutus,* the vertebral counts (median fin counts follow vertebral counts) are negatively correlated with pectoral fin counts. In contrast, these meristic characters are positively correlated within a given population; larger fish have more vertebrae and average more pectoral fin rays as well.

Johnsen indiscriminately attributed both kinds of variation to direct modification by the environment.

A further similarity between the results of Johnsen's investigation and the present study lies in the course of divergence of the fin index (calculated from his data). There is a geographic cline in the index which is minimal in the Baltic Sea and increases to the west and then independently south and north in the North Sea, but is maximal to the north.

In *Gillichthys mirabilis*, a genetic cline is also suggested by comparisons of population means of combined fin ray counts. Variation between year classes and a comparison of Salton Sea fish with their parental stock indicate that slower development is correlated with an increase in the total number of fin elements. If the developmental rates within the populations are altered by climatic temperatures, and this is a reasonable assumption, then the combined counts should decrease from north to south. But the combined counts are about the same for all populations, with a few exceptions, and the exceptions are obvious deviants.

One could argue for a cline of combined counts for the seven populations in California. But the counts increase, not decrease, steadily from San Francisco south to San Diego. Such differences from north to south could be attributed to increasingly saline water to the south, or to later spawning seasons to the north. Yet the northernmost habitat, the Alviso salt ponds, is highly saline, and spawning commences at about the same time throughout the range of *mirabilis*.

There seems to be homeostasis of the combined counts in spite of changes in latitude, since over the rest of the range of *mirabilis* the means are about the same from population to population. This suggests genetic compensation, or relatively complete acclimation of developmental rates. The most obvious deviant, the population from just north of San Felipe, is also atypical in body form.

The variance of the countable characters in each population is even more stable than the mean of the characters. It does not appear possible to estimate the respective roles of heredity and environment in producing this constancy.

Even though the means of the counts were found to shift within limits from year class to year class, the variances showed no statistical differences. The environmental changes responsible for the changes in mean counts, most likely temperature, apparently do not influence the variances. This would seem to indicate an intrinsic homeostasis where variability is concerned.

Photoperiod might determine variability. Day length is constant from year to year on the same day at a given location. Since the change in photoperiod over the spawning season increases faster at higher latitudes, one can demonstrate a positive, although perhaps false, correlation between degree of change in day length and variance. Interestingly, estimates of the variances of the different fins in populations of a different but closely related species, *Gillichthys seta* (Barlow, 1961*a*), fall directly in the midst of the corresponding data (Fig. 10) for *mirabilis*. Somewhat further aside, in two different populations of *seta* the measurements of four body parts, not counts, having different means had the same variances (Barlow, 1961*a*).

If the variance of each character is largely genetically determined, then the data indicate two different types of clines in *mirabilis*. Based on the variances, there would be a simple linear relationship, north to south, irrespective of whether the populations are situated on the Pacific Coast or on the east or the west coasts of the Gulf of California. The V-like arrangement deduced from the distribution of the means of the counts, the fin indices, and measurements of body parts have already been described and will be summarized below.

The possible relationship between the differential of the photoperiod and the variance cannot be considered as evidence for or against modification or genetic determination. Even though the environment originally may have induced the variance in question, the phenotype easily could have become genetically reinforced.

The kind and pattern of the differences found between the populations of *mirabilis* seem too complex to be accounted for on the assumption that the dissimilarities result chiefly from direct environmental modification. The most obvious part of the explanation is that the divergences

reflect the degree of physical separation between populations. The less the exchange of genetic material, the greater the opportunity for dissimilarities to arise and persist.

If we are to understand why the variation is in a particular direction and not random, then we must first seek correlations between environmental factors and the observed geographic cline. Temperature and illumination are the only obvious parameters suitable to such an inquiry. The only evidence available relates to temperature differences, so illumination will not be treated. This raises the problem, inherent in such an approach, of formulating a self-realizing assumption.

I have already pointed out the crude correlation between the clines of meristic characters reported on and the gradient of temperatures found late in the summer. In another article (Barlow, 1961*b*), I have argued that relatively stable differences in the means of counts between populations probably reflect physiological differences, most likely temperature responses, that are genetically determined. Changes in counts between populations, as suggested by Hubbs (1928), might constitute examples of the well-known Baldwin effect (Baldwin, 1896): phenotypic modification of the counts (resulting from physiological adjustment) becomes genetically augmented and characterizes the population. A similar argument might hold for the differences in variances that apparently are associated with different photoperiods.

Peculiarities of G. mirabilis *from the Salton Sea*

The Salton Sea is a saline lake situated in the Salton Sink, a northward extension of the Gulf of California basin. According to Carpelan (1958), it has a surface area of about 340 square miles, but a maximum and highly variable depth of only 12 m. The salinity of the water is about 33 ‰, although the Salton Sea is not of marine origin; it has been formed by the inflow and evaporation of Colorado River water. Relative to ocean water, sulfate (2.7 times more concentrated) and calcium (1.9) ions are especially abundant, whereas potassium (0.58) and magnesium (0.75) are appreciably less concentrated. The annual maximum and minimum surface water temperatures are usu-

ally about 36C and 10C, respectively. Great daily fluctuation in temperature occurs, especially in shallow water (Barlow, 1958).

The specimens of *mirabilis* from the Salton Sea differ from those on the outer coast in just the ways one would predict for fish whose growth had been drastically retarded. All fin ray counts and the vertebral counts are high (but the relationship between the fin counts is unchanged), supernumerary spiny rays are formed, scalation is incomplete, the head and its related parts are small, the fins are low, and the completion of the interorbital canal is delayed. Anomalies, such as a continuous slit for the anterior and posterior nares, an abbreviated postorbital canal, and flaps on the jaws, are holdovers of conditions usually seen only in postlarvae.

The unusual combination of salts in the water of the Salton Sea probably interferes with the development of the fish. The water temperatures are not to be considered responsible, for they are moderate during that period of early development when the characters are determined. Indeed, the temperatures are comparable to those of habitats along the sea coasts. Other water conditions (oxygen tension, pH, and illumination) also are similar to those encountered by naturally occurring populations. The Salton Sea fish at times are heavily infested with a monogenetic trematode, but so are coastal populations. Besides, many of the characters are determined before hatching and so could not be modified by debilitation caused by parasites (Hubbs, 1927).

The possibility exists, of course, that the *mirabilis* in the Salton Sea have diverged genetically, and that the structural differences are the result of such genetic change. The original stock consisted of merely 500 fish, of which only a fraction could have reproduced successfully. By chance alone, certain alleles must have been lost, others fixed, even if all 500 fish are assumed to have reproduced (Wright, 1951). The population expanded rapidly to a large number of fish, as did later introductions of other species. In a large population, genetic drift would no longer be operative (Wright, 1951). During the 25 years after introduction, selection has been effected, for the most part,

through the rigorous environment and through intraspecific competition.

If the gene pool of the Salton Sea fish has been altered, then the morphological changes might be due to such genetic differences. This cannot be known without rearing experiments. Experiments on the metabolic physiology of the adults suggest slight genetic divergence has taken place (Barlow, 1961c).

My opinion is that the morphological peculiarities of the fish from the Salton Sea can be ascribed primarily to direct modification caused by the chemical composition of the water in which they develop; the same could be said of the San Felipe fish from a saline pool.

Conclusions

The investigation of the species *Gillichthys mirabilis* has revealed a complex situation in which genetic divergence is evidently intertwined with phenotypic plasticity.

Over the range of *mirabilis,* the adaptive norms seem to shift gradually, but with some plateaus. A comparison of fin indices and means of the fin counts indicates the following arrangement: (1) Populations of *mirabilis* are nearly the same genetically on the California coast, though the Salton Sea and San Francisco populations may be somewhat distinct. (2) A genetic cline may exist on the outer coast of Baja California. (3) The fish from the lower region of the Gulf of California are similar to, but slightly different from, those on the outer coast of southern Baja California. (4) The populations found in the northern part of the Gulf have diverged from those of the southern part to a greater degree than can be accounted for, in a consistent manner, by environmentally induced changes.

Investigations of the body form of *mirabilis* support the conclusions based on countable characters. The body form of fish from California is about the same in each of the populations, although local differences exist. Fish from the Gulf of California, as a group, differ from those from California; no adult specimens were available from the outer coast of southern Baja California. Within the Gulf populations, fish in the upper northern region of the Gulf are separable from those in the southern region.

Thus *mirabilis* is seen as one widely ranging species whose geographic subdivisions are consistent with known faunal regions. For example, the fish fauna of San Francisco Bay is isolated from its southern counterpart, and the degree of differentiation of the *mirabilis* population there reflects this separation. The broad transition between faunas along the outer coast of Baja California also seems to be an area of transition for *mirabilis,* though more samples are needed from this region. Likewise, the morphological separation of the *mirabilis* of the Gulf from those of the outer coast is in keeping with the known distribution of this species. Finally, the division of *mirabilis* from the Gulf into northern and southern groups is in harmony with faunistic and oceanographic findings (Hubbs, 1960; Walker, 1960; Roden, 1958).

Subspecific names are not proposed for the geographic variants. Until more collections are available it would only create confusion to name the geographic forms as they are known at present. Even if they were better known, I doubt that subspecific names would be of utility here. None of the evidence suggests that any group, or groups, of populations is evolving into a distinct species. The findings indicate only that in this widely distributed species appreciable differences exist; these are thought to reflect adaptive changes.

SUMMARY

1. *Gillichthys mirabilis* Cooper is found in coastal sloughs from Central California south to near Cabo San Lucas, and then again in the central and northern parts of the Gulf of California. It has been introduced into the Salton Sea.

2. The fish spawn from about January to June and reach maturity within 1 year. The larvae have a brief pelagic phase, during which time the species is distributed to new habitats.

3. The head is shortest in specimens of *mirabilis* from the Salton Sea and most depressed in those from the Gulf of California. The length of the upper jaw and the height of the median fins are greatest in samples from the Gulf and least in those from the Salton Sea. Specimens from the upper Gulf region have the dorsal fins separated more than in *mirabilis* from elsewhere.

4. The scales are larger and the ventral area more scaled in specimens from the Gulf than in those from the outer coast. Scalation is noticeably reduced in fish from the Salton Sea.

5. Trends in means of meristic characters, from north to south along the Pacific Coast, and then from south to north up into the Gulf of California, are as follows: spiny dorsal fin—no change or slight increase; segmented rays of median fins—decrease; pectoral fin—increase; combined fin elements—irregular or no change; fin index (segmented dorsal plus anal rays, divided by pectoral rays, times 100)—decrease; pectoral fin asymmetry—decrease; vertebrae—no change.

6. The variance of the number of elements in each fin is a function of latitude, greater variance being associated with higher latitudes.

7. The means of the counts of the median fin are negatively correlated with the means for pectoral fin rays when the comparison is between the various populations. In successive year classes within a given population, however, changes in the number of rays in the median fins are associated with commensurate changes of the same sign in the counts of the pectoral fin rays. But within each year class there is no correlation between the number of pectoral fin and median fin rays.

8. All meristic characters have higher mean values in specimens from the Salton Sea, but the mean of their fin index accords with the Pacific Coast population from which they were derived. The Salton Sea fish are aberrant in many ways, evidently as a result of living in a marginal environment.

9. The conclusions based on these findings are condensed on the last page of the foregoing article.

REFERENCES

BALDWIN, J. M. 1896. A new factor in evolution. Amer. Nat. 30: 441–475, 536–553.

BARLOW, G. W. 1958. Daily movements of desert pupfish, *Cyprinodon macularius,* in shore pools of the Salton Sea, California. Ecology 39: 580–587.

———— 1961a. Gobies of the genus *Gillichthys,* with a comment on the sensory canals as a taxonomic tool. Copeia 1961: 423–437.

———— 1961b. Causes and significance of morphological variation in fishes. Syst. Zool. 10: 105–117.

———— 1961c. Intra- and interspecific differences in rate of oxygen consumption in gobiid fishes of the genus *Gillichthys.* Biol. Bull. 121: 209–229.

CARPELAN, L. H. 1957. Hydrobiology of the Alviso salt ponds. Ecology 38: 375–390.

———— 1958. The Salton Sea. Physical and chemical characteristics. Limnol. Oceanog. 3: 373–386.

GARTH, J. S. 1960. The biogeography of Baja California and adjacent seas, Part II. Marine biotas. Distribution and affinities of the brachyuran Crustacea. Syst. Zool. 9: 105–123.

GILBERT, C. H., and N. B. SCOFIELD. 1898. Notes on a collection of fishes from the Colorado Basin in Arizona. Proc. U. S. Nat. Mus. (20): 487–499.

HOEL, P. G. 1954. Introduction to Mathematical Statistics. 2nd ed. Wiley & Sons, New York. 331 pp.

HUBBS, C. L. 1921. Geographic variation of *Notemigonus crysoleucas*—an American minnow. Trans. Ill. Acad. Sci. 11: 147–151.

———— 1922. Variations in the number of vertebrae and other meristic characters of fishes correlated with temperature of water during development. Amer. Nat. 56: 360–372.

———— 1924. Studies on the fishes of the order Cyprinodontes, IV. The subspecies of *Pseudoxiphophorus bimaculatus* and *Priapichthys annectens.* Misc. Publ. Mus. Zool. Univ. Mich. (13): 17–23.

———— 1926. The structural consequences of modifications of the developmental rate in fishes, considered in reference to certain problems of evolution. Amer. Nat. 60: 57–81.

———— 1927. The related effects of a parasite on a fish. A retardation of early growth, the retention of larval characters and an increase in the number of scales. J. Parasit. 14: 75–84.

———— 1928. An hypothesis on the origin of graded series of local races in fishes. Anat. Rec. 41: 49. (Abstract.)

———— 1948. Changes in the fish fauna of western North America correlated with changes in ocean temperature. Sears Found. J. Mar. Res. 7: 459–482.

———— 1960. The biogeography of Baja California and adjacent seas, Part II. Marine biotas. The marine vertebrates of the outer coast. Syst. Zool. 9: 134–147.

———— and C. HUBBS. 1953. An improved graphical analysis and comparison of series of samples. Syst. Zool. 2: 49–57.

———— and L. C. HUBBS. 1945. Bilateral asymmetry and bilateral variation in fishes. Papers Mich. Acad. Sci. Arts and Letters 30 (1944): 229–310.

———— and K. F. LAGLER. 1949. Fishes of the Great Lakes Region. Cranbrook Press, Bloomfield, Mich. 186 pp.

JOHNSEN, S. 1936. On the variation of fishes in relation to environment. (Preliminary account.) Bergens Mus. Aarb. (4): 1–26.

MACGINITIE, G. E. 1939. The natural history of the blind goby, *Typhlogobius californiensis* Steindachner. Amer. Midl. Nat. 21: 489–505.

MARTIN, W. R. 1949. The mechanics of environmental control of body form in fishes. Univ. Toronto Stud. Biol. Ser. (58), Publ. Ontario Fish. Res. Lab. (70): 1–91.

RODEN, G. I. 1958. Oceanographic and meteorological aspects of the Gulf of California. Pacif. Sci. 13: 21–45.

———— and G. W. GROVES. 1959. Recent oceanographic investigations in the Gulf of California. Sears Found. J. Mar. Res. 18: 10–35.

SCHMIDT, J. 1919. Racial studies in fishes, II. Experimental investigations with *Lebistes reticulatus* (Peters) Regan. J. Genet. 8: 147–153.

SCHULTZ, L. P. 1927. Temperature controlled variation in the golden shiner, *Notemigonus crysoleucas.* Papers Mich. Acad. Sci. 7: 417–432.

SEYMOUR, A. H. 1956. Effects of temperature upon young chinook salmon. Dissertation Abstr. 16: 2249.

STARKS, E. C., and E. L. MORRIS. 1907. The marine fishes of southern California. Univ. Calif. Publ. Zool. 3: 159–251.

TÅNING, A. V. 1952. Experimental study of meristic characters in fishes. Biol. Rev. 27: 169–193.

TAVOLGA, W. N. 1954. Reproductive behavior in the gobiid fish *Bathygobius soporator.* Bull. Amer. Mus. Nat. Hist. 104: 431–459.

VLADYKOV, V. D. 1934. Environmental and taxonomic characters of fishes. Trans. Roy. Canad. Inst. 20: 99–140.

WALKER, B. W. 1960. The biogeography of Baja California and adjacent seas, Part II. Marine biotas. The distribution and affinities of the marine fish fauna of the Gulf of California. Syst. Zool. 9: 123–133.

WEISEL, G. F. 1947. Breeding behavior and early development of the mudsucker, a gobiid fish of California. Copeia 1947: 77–85.

———— 1948. Relation of salinity to the activity of the spermatoza of *Gillichthys,* a marine teleost. Physiol. Zool. 21: 40–48.

WRIGHT, S. 1951. The genetical structure of populations. Ann. Eugen. 15: 323–354.